Strapline: Soil microbes

Title: Traits track taxonomy

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Standfirst: A novel isotope technique shows that compared to ecosystem type, evolutionary history explains more variation in bacterial growth traits along an elevation gradient. This knowledge could help move microbial ecologists toward improved predictive models of soil processes.

Bacteria and Archaea account for the vast majority of genetic diversity of life on Earth[1]. Studying such an enormous trove of microbes—and the specific roles they play—has been a major challenge for microbial ecologists. In this issue of *Nature Ecology and Evolution*, Morrissey et al.[2] tackle diverse microbial communities with a powerful new isotope technique in soils of the southwestern United States. The approach reveals that evolutionary history explains much of the variation in microbial growth traits.

The link between specific organisms and the functioning of ecological communities has fascinated ecologists for centuries. So-called "structure-function" relationships are the linchpin needed to predict ecosystem functioning in a changing climate, for example[3], and here the authors aimed to test if key determinants of microbial functioning were similar across different environments. One hypothesis is that phenotypic characteristics, or traits, are more similar for more closely related microbes[4]. Such consistency would be convenient because ecologists could predict ecosystem functioning based on which microbial taxa are present. If traits reflect evolutionary history, taxonomic information might be sufficient to build a predictive model of ecosystem processes such as carbon cycling. And advances in high-throughput DNA sequencing mean that taxonomic information is easy to get for almost any microbial community.

What's harder to get is accurate data on microbial traits, and how traits vary under different environmental conditions, especially for intact communities in the field. Previous studies have measured traits on pure cultures of microbes[5], but this work is painstaking and subject to methodological limitations. There are some emerging approaches for analyzing the traits of whole microbial communities, but these measurements are low in taxonomic resolution[6]. Using a new technique known as quantitative stable isotope probing, or qSIP, Morrissey et al. measured growth and resource assimilation traits on intact bacterial communities in soils across an elevation gradient in Arizona, USA. The method requires an ultracentrifuge and some clever math combined with modern DNA sequencing tools, but what results is a detailed profile of growth and carbon assimilation rates for every resident bacterial group that can be sequenced from a given soil.

With sites along the elevation gradient ranging from dry grassland to coniferous forest, ecosystem type was a key variable that represented substantial environmental variation in the study design. Evolutionary history—represented as taxonomic assignment to groups like phylum and family—was the other main experimental variable.

A nested analysis of variance gave a clear result. Taxonomy, and the evolutionary history it represents, explained a much larger fraction of the variation in bacterial traits than ecosystem type (Fig. 1). Whereas ecosystem explained 20% of the variation at most, taxonomy explained up to 65%. Family and bacterial phylotype (roughly the species level) accounted for most of the variation attributed to taxonomy.

The taxonomic level accounting for the most variance can vary widely by trait[7]. Complex traits like methane production that require many genes are often deeply conserved, for example at the order level. More simple traits—like the assimilation of carbon substrates—involve fewer genes and are generally conserved at the genus to phylotype level in culture-based studies. Morrissey et al.'s analysis suggests that rates of growth and glucose assimilation are also relatively simple traits for bacteria growing in soil.

Growth and carbon assimilation traits are important in microbial communities. Growth rate reflects the physiological balance between building biomass and expending resources to survive. Carbon assimilation rate gives information about potential resource use and competitive ability. The holy grail for structure-function researchers is to apply trait data like Morrissey et al. collected to predict ecosystem functioning. Still, there is a long way to go. The empirical data would have to be incorporated into a mathematical model, and such a model would require much more information.

Although they analyze soils from distinct ecosystem types, Morrissey et al. did not address how growth traits respond to abiotic conditions like temperature and soil moisture. That kind of data is needed to build dynamic models in which traits and functions change realistically with climate and other drivers. Another unresolved issue for prediction is how to represent the taxonomic diversity of microbes in an ecosystem model. The authors nicely demonstrate that different bacterial families and phylotypes have distinct traits that relate to carbon and nutrient cycling. But even the most sophisticated ecosystem models only include a handful of different microbial groups[8], not the hundreds found in the Arizona soils. Modelers need a scheme for lumping this taxonomic diversity into a manageable number of groups or representing it through continuous distributions. Overall, progress on prediction will require a lot more cross-talk between microbial empiricists and ecosystem modelers[8].

Even though accurate predictive models may elude us, Morrissey et al.'s results still stand out as an important contribution. Ecologists have long known that traits correspond to taxonomy in macroscopic organisms like trees and birds[9,10]. Pine trees have needles regardless of whether they grow in Canada or Central America. Yet finding the same pattern with microbes was no guarantee. Bacteria can evolve and exchange genes rapidly[11,12], so bacterial traits might have shown very short evolutionary histories. Any

differences among taxa could have been washed out quickly, leaving the soil environment as the dominant force determining bacterial traits.

But that's not the case. Thanks to Morrissey et al., we now know that a *Bacillus* keeps its high growth rate just as a pine tree keeps its needles, no matter where it grows.

Competing Interests
The author declares no competing interests.

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Figure 1. Using a new technique with isotope labels, Morrissey et al. show that evolutionary history explains more variation in soil bacterial traits than soil conditions in ecosystems across an elevation gradient. The link between taxonomy and traits like growth rate and carbon assimilation could be useful in modeling soil processes under a changing climate. Colored areas approximate the proportion of variance explained by ecosystem type (green) or taxonomy (blue) for bacterial growth rates (a) or carbon assimilation rates (b) with added growth substrates.